

Resistance to *Bemisia tabaci* in tomato species and hybrids and its association with leaf trichomes

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Abstract Chemical insecticides comprise the most widely used method of tomato pest control. Genotypes resistant to pests such as the silver leaf whitefly *Bemisia tabaci* may contribute towards the decreased use of insecticides to protect the environment. Leaf trichomes play a role in imparting resistance to pests, and exploiting intraspecific and interspecific variability for leaf trichomes in the tomato gene pool is an alternative to speed up introgression of resistance into improved lines or cultivars. We assessed the levels of whitefly resistance and trichome morphology/density in an array of accessions of the tomato gene pool and their hybrids with a tomato cultivar. A commercial cultivar (*S. lycopersicum* cv. Redenção), six wild species accessions, two *S. lycopersicum* var.

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Agricultural Research Center, Plant Pathology Research Institute, 9 Gamaa St., Giza 12619, Egypt e-mail: youssefeladawy@yahoo.com cerasiforme genotypes, and eight intra and interspecific F_1 hybrids were tested. The accessions LA 1401 (S. galapagense), AF 19684 (S. peruvianum), PI 127826 (S. habrochaites var. hirsutum), PI 134417 (S. habrochaites var. glabratum), LA 716 (S. pennellii), and RVTC 03 (S. lycopersicum var. cerasiforme) genotypes showed a higher density of glandular trichomes and carried the highest levels of whitefly resistance than the commercial cultivar. Segregating generations from their crosses with the cultivar may be promising sources to select plants with both higher density of glandular trichomes and resistance to whiteflies. Populations derived from S. lycopersicum var. cerasiforme' RVTC 03', which is part of intraspecific S. lycopersicum variability, maybe a more convenient source of pest resistance than those derived from interspecific crosses to obtain pestresistant tomato cultivars.

Keywords Solanum lycopersicum · Glandular trichomes · Wild tomato · Whitefly resistance

Introduction

The tomato crop is plagued by an array of arthropod pests, which unchecked may cause considerable yield and quality losses (Mahmoud et al. 2020; Moerkens et al. 2020). Chemical pesticide sprays are the most

often used method of pests/disease control but can lead to increased costs, environmental damages and harm to consumer's health (Lachhab et al. 2015; Youssef et al. 2019). The use of pest-resistant tomato cultivars may represent a less costly and environmentally safer alternative to chemical control (Zanin et al. 2018; Neiva et al. 2019).

Whitefly (Bemisia tabaci biotype B) is currently one of the major tomato pests worldwide (Firdaus et al. 2012; Yule et al. 2019; Jafarbeigi et al. 2020). Its direct injury occurs by the insect sucking the sap, and triggering physiological disorders in tomato plants (Firdaus et al. 2012; Neiva et al. 2019), while indirect damage occurs through the transmission of begomovirus, as well as secretion of sugars that remain on the surface of the plant epidermis and may lead to the appearance of sooty mold (Capnodium spp.) (Andrade et al. 2017; Gouveia et al. 2018). These damages lead to yield losses, as well as to irregular fruit ripening that renders fruit unsuitable for fresh consumption or processing. The development of whitefly-resistant cultivars can therefore be considered a tomato breeding priority (Firdaus et al. 2012; Neiva et al. 2019). The main physic-chemical plant factors conferring whitefly resistance are reported to be the trichomes (Glas et al. 2012; Andrade et al. 2018).

Trichomes are essential as natural plant defenses especially against phytophagous insects (Silva et al. 2019). They consist of epidermal structures similar to hairs that can influence insect behavior and consequently confer pest resistance (Rakha et al. 2017). The different types of trichomes are classified based on the presence or absence of trichome glandular head, stalk length, cell number and base cell number properties (Luckwill 1943). Tomato trichomes are usually categorized as glandular types I, IV, VI and VII and nonglandular types II, III and V (Luckwill 1943; Channarayappa et al. 1992). Glandular trichomes release sticky and/or toxic exudates, which may cause pest death (Andrade et al. 2018). Additionally, non-glandular trichomes may act by mechanical means and by forming a barrier that prevents pest contact with plant tissue (Simmons and Gurr 2005).

Levels of resistance to whitefly are highly variable among accessions of the tomato gene pool (Firdaus et al. 2012). Genotypes of wild tomato species *S. pennellii* (Resende et al. 2002) and *S. habrochaites* (Maluf et al. 2001) are noteworthy concerning the introgression of pest resistance characteristics in cultivated tomatoes. However, many horticultural undesirable genes are involved in the process of introgression of whitefly resistance from wild parents into commercial cultivars (Momotaz et al. 2010). Therefore, exploiting resistance derived from accessions that are taxonomically closer to S.lycopersicon may contribute to a reduction in time and costs necessary to obtain improved resistant cultivars. The species S. pimpinellifolium and S. galapagense are closer to S. lycopersicum in comparison with S. pennellii and S. habrochaites (Peralta et al. 2008). S. lycopersicum var. cerasiforme was also considered to be promising as a donor of resistance genes (Lucini et al. 2016). Considering the wide genetic variability of tomatoes, relatively few studies exploring potential pest resistance are available (Firdaus et al. 2012). Further studies related to the presence of glandular trichomes and their relation with whitefly resistance in specific wild or feral accessions and F₁ their hybrids with S. lycopersicum would provide important information for resistance introgression. Further studies are needed on the presence of glandular trichomes in putative whitefly-resistant accessions, and their relationship with resistance and the levels of resistance eventually found in their hybrids with S. lycopersicum.

The objectives of this work are: (a) to assess the comparative levels of whitefly resistance in wild tomato accessions, in their hybrids with a commercial *S. lycopersicum*, and the possible relationship with the presence of glandular trichomes; (b) to identify putative sources of whitefly resistance in accessions taxonomically close to *S. lycopersicum*, that could be deployed more efficiently in the process of introgression of resistance to obtain improved cultivars.

Materials and methods

Genotypes and experimental design

Six wild tomato species were assessed (*S. pimpinel-lifolium* 'AF 26970', *S. galapagense* 'LA 1401', *S. peruvianum* 'AF 19684', *S. habrochaites* var. *hirsu-tum* 'PI 127826', *S. habrochaites* var. *glabratum* 'PI134417' and *S. pennellii* 'LA 716') along with two *S. lycopersicum* var. *cerasiforme* genotypes ('RVTC 03' and 'RVTC 66'), one *S. lycopersicum* line (cultivar Redenção); and eight hybrids [F₁(Redenção × AF 26970), F₁(Redenção × LA 1401), F₁(Redenção

× AF 19684), F_1 (Redenção × PI 127826), F_1 (Redenção × PI 134417), F_1 (Redenção × LA 716), F_1 (Redenção × RVTC 03) and F_1 (Redenção × RVTC 66)]. A randomized block design was used, with five replications with eight plants each. All interspecific F_1 hybrids bore small fruit (ca. 1–2 cm diameter), and the only ones showing mature fruit colors similar (red or orange) to *S. lycopersicum* were those with the species that are more closely related to the latter, i.e., *S. pimpinellifolium* and *S. galapagense*.

Sowing was carried out in expanded polystyrene trays with 200 cells containing a commercial substrate based on bio-stabilized pine bark. Trays were maintained in a greenhouse until the date of transplant. 'Redenção', 'RVTC 03', 'RVTC 66', 'AF 26970' and 'AF 19684', as well as the F₁hybridswere sown in the same date, while genotypes LA 1401, PI 127,826, PI 134,417 and LA 716 were sown ten days before, due to expected differences in germination and emergence. Seedlings were transplanted to 8 dm³ pots at the stage of 4-5 fully expanded leaves. The pots containing a commercial substrate based on bio-stabilized pine bark. Base fertilization with 2 g of N, 3 g of P, 3 g of K, 3 g of Ca, 1.8 g of Mg and 1.5 of S per pot was used. The plants were irrigated as needed with the use of micro-drippers. No phytosanitary sprayings (insecticides or fungicides)were carried out during plant growth and development.

Assessment of resistance to whitefly *Bemisia* tabaci

At the onset of flowering (30 days after transplanting) plants were assessed for resistance to whitefly in a greenhouse test under free choice conditions. A total of 150 non-sexed B. tabaci biotype B whitefly adults were released per plant. Attractiveness was assessed 24, 48 and 96 h after insect release. With the aid of a mirror, the number of adults present on the abaxial surface of three previously marked leaflets in the upper, middle and lower thirds of each plant was counted (Baldin et al. 2007). Whitefly egg and nymph counts were performed in quadruplicate on the 28th day after infestation. Three fully expanded young leaflets were collected during each evaluation, one from each third part (upper, middle and lower) of each plant. The leaflets were properly identified, placed in a gearbox and sent to the laboratory. The number of live eggs and nymphs present on the abaxial faces of each leaflet was counted with the aid of a stereoscopic binocular microscope (Olympus bh2), in a 4 cm² area, excluding the central rib.

Leaf trichome identification and counts

Four young leaflets were removed from the upper third of each plant for trichome enumeration and identification. Slides were mounted in quadruplicate with paradermic cuts on the abaxial and adaxial surfaces for each recently collected leaflet and subsequently fixed with carbon tape on a metallic support. A 5 mm²area was analyzed using a scanning electron microscope (Tescan® Vega3 HV) at 30 kv. Leaflet surfaces were photographed to facilitate length observations and identification of the presence or absence of gland(s) at the apical end of the leaf trichomes, as well as their shape. Based on these characteristics, trichome identification was carried out according to Channarayappa et al. (1992).

Data analyses

The data related to trichomes and whitefly resistance were subject to using the log (x + 1) transformation. Normality and homogeneity of residual variance assumptions were confirmed, the data were subjected to an analysis of variance (ANOVA). Means were subjected to statistical tests when the F test was significant, to differentiate and identify the most promising genotypes. Spearman correlations were calculated between glandular trichomes, non-glandular trichomes, number of adults 96 h after infestation, number of eggs, and number of whitefly nymphs. All analyses were performed using the GENES software (Cruz 2013).

Results

Trichome morphology and density

The most frequently observed glandular trichomes were IV and VI types, with higher numbers on abaxial leaflet surfaces (Table 1). All genotypes, except for 'AF 26970', F_1 (Redenção × RVTC 66) and F_1 (Redenção × AF 26970), displayed a higher total abaxial density of glandular trichomes (types I + IV + VI + VII) than the commercial *S.lycopersicum* cultivar

Genotype	Adaxial leaf	f surface			Abaxial leaf surface					
	Non- glandular 360.56	Glandul	ar		Non-	Glandular				
		IV	VI	I + IV + VI + VII	glandular	IV	VI	I + IV + VI + VII		
Redenção (R.)		12.56	0.00	12.56	492.44	8.50	0.00	8.50		
RVTC 03	354.33	12.83	0.00	12.83	347.67*	27.56*	0.00	27.56*		
RVTC 66	347.50	15.33	0.00	15.33	400.56*	17.56*	25.33*	42.99*		
AF 26970	132.50*	0.00	0.00	0.00	315.00*	0.00	0.00	0.00		
LA 1401	10.11*	37.50*	22.22*	60.00*	7.56*	202.44*	10.88*	213.32*		
AF 19684	230.56*	0.67	122.33*	123.00*	120.22*	0.00	327.50*	327.50*		
PI 127826	7.50*	85.00*	60.67*	170.11*	2.89*	312.89*	42.33*	367.45*		
PI 134417	20.22*	0.00	37.22*	37.22*	155.00*	20.33*	105.89*	142.33*		
LA 716	15.56*	65.33*	0.00	65.33*	7.50*	167.67*	0.00	167.67*		
$R. \times RVTC$ 03	375.89	17.44	0.00	17.44	410.56*	20.89*	17.44*	38.22*		
R. × RVTC 66	335.44	17.89	0.00	17.89	400.00*	12.56	0.00	12.56		
R. × AF 26970	72.33*	12.50	0.00	12.50	90.56*	0.00	0.00	0.00		
R. × LA 1401	215.45*	10.22	35.78*	46.00*	390.56*	20.56*	97.67*	118.23*		
R. × AF 19684	365.22	2.50	5.00	7.50	477.50	5.89	47.89*	53.78*		
R. × PI 127826	12.88*	40.20*	7.89	53.09*	102.33*	22.33*	30.33*	55.56*		
R. × PI 134417	305.44*	10.33	25.11*	35.44*	462.77	10.44	30.44*	40.88*		
R. × LA 716	187.45*	30.56*	0.00	30.56*	287.23*	82.11*	0.00	82.11*		

Table 1 Trichome density (per 5 mm²) on leaf surfaces per tomato species genotypes and hybrids

*Means differ from Solanum lycopersicum cultivar Redenção (Dunnett's test. $P \leq 0.05$)

Redenção (P < 0.05). The highest abaxial density of type IV and VI trichomes compared to 'Redenção' was observed in genotypes PI 127826 (312.89 per 5 mm²) and AF 19684 (327.50 per 5 mm²), respectively. However, 'AF 19684' displayed only type IV trichomes, on abaxial leaflet surfaces. The commercial cultivar Redenção presented the highest density of non-glandular trichomes on the same surface (492.44 per 1 mm²) (Table 1).

On the adaxial leaflet surface, the highest glandular trichome densities were observed (types I + IV + VI + VII) in genotypes LA 1401, AF 19684, PI 127826, PI 134417, LA 716, F_1 (Redenção × LA 1401), F_1 (Redenção × PI 127826), F_1 (Redenção × PI 134417) and F_1 (Redenção × LA 716) (P < 0.05). The highest densities of type IV and VI trichomes on the adaxial leaflet surface were observed in 'PI 127826' (85.00 per 5 mm²) and 'AF 19684' (122.33 per 5

mm²), respectively. Non-glandular trichome densities in the commercial cultivar Redenção did not differ those found in 'RVTC 03', 'RVTC 66', F1(Redenção \times RVTC 03), F₁(Redenção \times RVTC 66) and F₁(Redenção \times AF 19684) (Table 1). Type VI trichomes were not found in the adaxial surface either in 'RVTC03', 'RVTC66', 'AF26970', 'LA716', or in their hybrids with Redenção. Type IV trichomes neither were nor present in 'AF26970' and in 'PI 134417's adaxial surfaces, and were present in low densities in AF19684, and in the hybrids with these three accessions. Type IV trichomes were not present in the abaxial surfaces of genotypes AF26970, AF19684', and in F_1 (Redenção × AF 26970), and Type IV trichomes were not present in'RVTC03', 'AF26970', 'LA716', or in the hybrids F_1 (Redenção × RVTC66), F_1 (Redenção × AF26970) and F_1 (Redenção \times LA716).

Assessment of resistance to whitefly *Bemisia* tabaci

In the insect free-choice trials, RVTC 03, AF 19684, LA 716, LA 1401, PI 127826 and PI 134417 genotypes and their respective hybrids with Redenção presented an adult whitefly infestation of ≤ 1 per 4 cm². No whitefly adults in the LA 716, LA 1401 and PI 127826 genotypes were observed at 24, 48 and 96 hours after infestation. In contrast, 'Redenção', 'RVTC 66', 'AF 26970', F_1 (Redenção × RVTC 66) and F_1 (Redenção \times AF 26970) grouped as the most susceptible genotypes (P < 0.05), due to the higher presence of whitefly adults (Fig. 1). At 28 days after infestation, 'LA 716', 'LA 1401', 'PI 127826', 'AF 19684', 'PI 134417', F_1 (Redenção × LA 1401), F_1 (Redenção × LA 716) and 'RVTC 03' showed the lowest number of eggs and whitefly nymphs (P < 0.05). The highest egg density was observed in the interspecific hybrid F_1 (Redenção × AF 26,970), while the highest nymph density was detected in AF 26,970 (Fig. 2).

Association between trichomes and whitefly resistance

Table 2 showed that the determined parameters were significantly correlated. In particular, glandular trichome densities were negatively correlated with non-glandular trichomes (r = -0.56), number of adults (r = -0.89), number of eggs (r = -0.72), and number of nymphs (r = -0.88).In addition, non-glandular trichomes were positive correlated with number of eggs (r = 0.63) and nymphs (r = 0.51). Additionally, positive correlations were detected between the number of whitefly adults, eggs, and nymphs (Table 2).

Discussion

One of the objectives of the present research was to exploit resistance to whitefly observed in a sample of the tomato gene pool and verify its association with leaf trichome morphology and density. The trichome morphology of both cultivated and wild tomato species has been well characterized (Luckwill 1943; Channarayappa et al. 1992; Silva et al. 2019). However, considering the genetic variation among tomato species and their potential use in improving cultivated genotypes, there is still much to be explored regarding the trichome-related parameters (Zeist et al. 2018a). Variations between trichome types and densities in tomato species and hybrids were detected. Trichome characteristics and the potential of glandular trichomes in the breeding of commercial tomato plants aiming resistance for pests have been reported in populations derived from crosses of S. lycopersicum with S. galapagense 'LA-1401' (Andrade et al. 2017), with S. habrochaites var. hirsutum 'PI 127826' (Oliveira et al. 2018), with S. habrochaites var. glabratum 'PI 134417' (Neiva et al. 2013) and with species S. pennellii 'LA-716' (Dias et al. 2019). Our results reinforce these previously reported whitefly resistances of 'LA-1401', 'PI 127826', 'PI 134417' and 'LA-716', and their associations with glandular trichomes. However, trichome-related characters in 'AF 26970' (S. pimpinellifolium), 'AF 19684' (S. peruvianum), 'RVTC 03' and 'RVTC 66' (S. lycopersicum var. cerasiforme) genotypes were not reported previously. While the whitefly resistant accessions LA1401, PI 127826 and PI134417 contain both type IV and type VI trichomes, the also resistant 'LA-716' contains type IV glandular trichomes only, and 'AF 19684'almost exclusively type VI trichomes (Table 1).

Our results showed that the *S. lycopersicum* var. *cerasiforme* accessions 'AF 19684' and 'RVTC 03' are potential sources of genes to obtain improved tomato lines with whitefly resistance. In 'RVTC 03', however, resistance may not be explained by higher densities of glandular trichomes, because they are even lower than those found in the whitefly-susceptible 'RTVC66'.

The use of the interspecific variability of the LA 1401, PI 127826, PI 134417 and LA 716 genotypes in tomato breeding has previously reported (Neiva et al. 2013; Silva et al. 2019), however, only feasible in the long term and a very laborious process (Zeist et al. 2018a). This is due to the non-commercial patterns of these wild genotypes and the morphological differences in *S. lycopersicum* (Zeist et al. 2020). Thus, in the incorporation of genes related to trichomes and resistance to pests, successive cycles of backcrossing and selection are necessary to obtain advanced lines with good commercial standard (Neiva et al. 2013; Zeist et al. 2018a). The same aspect is valid to the AF 19684 accession from *S. peruvianum* and its Redenção hybrid (Zeist et al. 2018a, b, 2020), which



Fig. 1 Number of whitefly (*Bemisia tabaci*) adults in tomato species and hybrids at 24 (a), 48 (b) and 96 (c) hours after infestation (means followed by the same letters in belong to the same group by the Scott Knott test, P < 0.05)

demonstrated potential in generating whitefly-resistant genotypes with a higher density of type VI glandular trichomes. While testing 26 wild accessions that differed from the ones in our study, Firdaus et al. (2012) identified among them both whitefly susceptible and whitefly resistant accessions, with the greatest resistance potential in *Solanum galapagense* 'PRI95004/PY8027'. Resistance in the latter accession was associated with type IV trichomes. Neither *S*. *lycopersicum* var *cerasiforme* nor interspecific hybrids were tested by these authors. In the present work, a different wider array of wild species were tested, and we report that some genotypes bear only type IV or type VI trichomes and that the trichome types present on the abaxial and adaxial leaf surfaces may differ.

Significant negative correlations between glandular trichomes and the number of whitefly adults, eggs and nymphs indicated that trichomes were associated with



Fig. 2 Number of whitefly (*Bemisia tabaci*) eggs (a) and nymphs (b) in tomato species and hybrids at 28 days after infestation (means followed by the same letters in belong to the same group by the Scott Knott test, P < 0.05)

Table	2	Spearman	correlati	ons betv	veen gla	ndular	trichor	nes, no	n-glandul	ar tric	chomes,	numbe	er of	whitefly	i (Bemisia	tabaci)	in
adults	96	h after in	festation,	number	of white	fly egg	s and r	number	of nymph	ns in t	omato s	pecies	genot	types an	d hybrids		

	Non-glandular trichomes	Glandular trichomes	Number of adults	Number of eggs
Glandular trichomes	- 0.56*	-	_	-
Number of adults	0.45 ^{ns}	- 0.89**	_	_
Number of eggs	0.63**	- 0.72**	0.81**	-
Number of nymphs	0.51*	- 0.88**	0.86**	0.70**

**Significant at the 0.01 level

*Significant at the 0.05 level

^{ns}Non-significant at the 0.05 level

whitefly resistance, as genotypes with a higher number of granular trichomes presented low incidences of whitefly adults, eggs and nymphs. Whitefly resistance is associated with allelochemical levels present in glandular trichomes (Andrade et al. 2017; Neiva et al. 2019), naturally occurring chemical substances with antagonistic action toward pests. However, this may not be the only mechanism imparting insect resistance: the glandular trichome densities in the whitefly resistant 'RTVC03' are comparable or lower than in the whitefly susceptible 'RTVC66'.

Acyl sugars, sesquiterpenes and methyl ketones, among others, are noteworthy among several allelochemicals found in wild tomato species (Neiva et al. 2013). Acyl sugars, such as acylglucoses and acylsucroses, have been reported in the leaf trichomes of the *S. pennellii* 'LA 716' (Dias et al. 2019) and the *S. galapagense* 'LA 1401' (Silva et al. 2019). Sesquiterpenes, mainly zingiberene, have been reported in the *S. habrochaites* var. *hirsutum* accession PI 127826 (Oliveira et al. 2018) and methyl ketone, 2-tridecanone, in the *S. habrochaites* var. *glabratum* accession PI 134417 (Neiva et al. 2013; Zeist et al. 2018a). These allelochemicals may lead to antibiosis and/or antixenosis plant responses against pests (Simmons and Gurr 2004; Zeist et al. 2018a).

Positive and significant correlations between nonglandular trichomes and the number of whitefly eggs and nymphs indicated that trichomes were not associated with whitefly resistance. Besides, a negative correlation between glandular and non-glandular trichomes was also found by Andrade et al. (2018), who suggested an ontogenetic relationship between these types of trichomes, where the presence of alleles responsible for allelochemical contents would be involved in the development of glandular structure at the tip of the trichomes.

It's well known that non-glandular trichomes do not produce toxic exudates, so plant protection, if any, is only physical (Cho et al. 2017). 'RVTC 66', 'AF 26970', 'Redenção', F_1 (Redenção × RVTC 66) and F_1 (Redenção × AF 26970), which presented a lower number of glandular trichomes, displayed a higher incidence of whitefly eggs and nymphs (Table 1; Figs. 1, 2).

The potential of the RVTC 03 genotype to increase whitefly resistance in cultivated tomatoes is very promising. 'RVTC' 03 is part of the intraspecific S. lycopersicum variability (var. cerasiforme), producing fruits with a pattern similar to commercial varieties (Preczenhak et al. 2014). Because feral forms of var. cerasiforme are reported to be the more direct ancestors of the cultivated forms of S. lycopersicum (Nesbitt and Tanksley 2002; Bai and Lindhout 2007; Peralta et al. 2008), their genetic proximity to the latter makes accessions such as 'RVTC 03' a more convenient source of resistance for deployment in breeding programmers than other similarly resistant accessions found in S. pennellii, S. habrochaites and even in S. galapagense. Deployment of 'RVTC 03' as a source of resistance may represent the need for a smaller number of backcrosses towards the susceptible horticultural acceptable parent, thereby reducing time and resources needed to obtain an improved resistant tomato line (Rodríguez et al. 2010). The potential for using *S. lycopersicum* var. *cerasiforme* in the breeding of cultivated tomatoes has been commonly reported for several purposes (Ranc et al. 2008; Rodríguez et al. 2010; Leiva-Brondo et al. 2016). Thousands of genotypes are part of the *cerasiforme* variety, and their peculiarities should be further studied (Ranc et al. 2008; Islam et al. 2012; Preczenhak et al. 2014). This is evident when observing the contrasting differences between 'RVTC 03' and 'RVTC 66' relative to trichome types/densities and whitefly resistance, in which only the former demonstrated the potential for deployment in a resistance breeding.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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